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EFFECT OF THE SPACE-FLIGHT FACTORS OF THE FUNCTIONAL STATE OF THE VESTIBULAR ANALYZER. REVIEW OF THE LITERATURE

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EFFECT OF THE SPACE-FLIGHT FACTORS OF THE FUNCTIONAL STATE OF THE VESTIBULAR ANALYZER. REVIEW OF THE LITERATURE

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ABSTRACT. Review of bibliography dealing with the effects of vibration, acceleration, and ionizing radiation on the functions of the vestibular analyzer, covering papers published through 1965. The review shows that the vestibular analyzer is responsible for various disorders in motor coordination and spatial orientation during parabolic and orbital flights and points out a general lack of information on many aspects of the subject.

The Functional State of the Vestibular Analyzer under Conditions of Parabolic and Orbital Flights

It seems unnecessary to analyze in detail the existing bibliographic material, since the problem under consideration /9** is very broad and there already are reviews on its various aspects (Yazdovskiy, Kas'yan, and Kopanev, 1964; Yazdovskiy and Yemel'yanov, 1964; Gazenko, Kas'yan et al.* 1964; Luk'yanova, 1964a; Livshits, 1961, 1964, etc.). Our task was to give a general review and a brief analysis of the available material.

During vertical, parabolic, and orbital flights, the organism of animals and man shows a number of changes connected with disturbance of the vestibular functions. Most frequently occurring among such changes are motor coordination, vestibular-sensory, and vestibular vegetative deviations. Disturbances of movement coordination are usually not pronounced. Most investigators note that motor acts are executed normally under flight conditions, and that the working capacity of subjects is not impaired (Antipov, Bayevskiy, Gazenko et al., 1962; Volynkin, Saksonov, 1964; Yuganov, Kas'yan, Gurovskiy et al., 1961; Gerathewohl, 1960; Lomonaco et al., 1957; Ballinger, 1952; etc.). However, certain deviations still occur, particularly in case of finely coordinated movements. More pronounced deviations have also been observed in animals, especially in small ones. Under conditions of weightlessness, mice and rats rotate around the longitudinal axis of their bodies. Rapid, disorderly movements gradually slow down and become somewhat normalized (Volynkin, Saksonov, 1964;

** Numbers in the margin indicate pagination in the foreign text.

* Translator's note: Reference citations were not included among the pages translated.

Gazenko, Chernigovskiy, Yazdovskiy, 1964; Yazdovskiy, Yuganov, Kas'yan, 1960). Turtles had difficulties in grasping food during flights (Beckh, 1954). It was observed by Graybiel and co authors (Graybiel, Holmes et al. 1959) that small monkeys of the Saimiri species showed increased movement frequency at the end of the weightless period. During parabolic flights, some disturbance of voluntary motion coordination has been observed in man (Yuganov, Kas'yan, et al., 1962; Whitside, 1961; Chkhaidze, 1962b). There was a tendency toward retardation in the speed of performing assigned motor acts (Kas'yan, Kopanev, Yuganov, 1964; Yuganov, Kas'yan, Gurovskiy et al., 1961). Decrease of the accuracy of movements during parabolic flights is detected by special tests. L.A. Kitayev-Smyk (1963a) used tests involving writing and target shooting. The accuracy of fine motions decreased, hits in shooting shifted upward and to the right. The number of errors in setting marker arrows increased 3-4 times. Small changes in the "writing sample" and in the operation of a special coordinograph were detected by Ye. M. Yuganov et al. (1961). If subjects were in a fixed position, movements were executed more quickly and accurately (Kas'yan, Kolosov et al., 1966). Some difficulties of the subjects in hitting a target with the hand (hits were 1 cm above and to the right of the target) were noted by Gerathewohl and Stallings (1957), and by Ballinger (1952). In Bekh's tests (1954) the subjects, tested under conditions of weightlessness in parabolic flights, sketched small crosses along the diagonal from the top downward in special squares. Without visual control, after the third cross a deviation from the drawing line of 90° with respect to the upper right-hand corner was noted. Experiments for the determination of movement coordination were conducted in a specially constructed "Roman tower." The test subjects had to hit a target 15 cm in diameter with a pencil in a certain rhythm. A marked dispersion of hits over the entire target, as compared with the control, was noted (Lomonaco et al., 1957). /10

Similar phenomena were also observed during orbital flights in satellites. No basic disorders in motor coordination were noted in the astronauts. Ability to execute finely coordinated movements was checked by special tests. With and without visual control, the astronauts had to stretch their arms in front of them and touch an instrument on the control panel.

A three-loop spiral and two stars in a continuous line were also drawn in the logbook. During the flight in the "Voskhod" spacecraft, the graphic test consisted in the drawing of small circles in a horizontal, a vertical and a

diagonal direction. The coordination of movements was effected fairly easily and accurately during the entire flight. Changes in handwriting (notes in log-books) resulted mainly from the unusual external conditions of writing; analysis of the handwriting did not show any symptoms of functional disorder of the central nervous system. Under conditions of weightlessness, the values of the force component in the movements changed. The greatest changes in handwriting were /11
observed at the beginning and at the end of flight. In drawing stars and spirals in the first tests, some differences from the control on earth sometimes appeared. In the case of head turns under weightlessness, a deviation of the outstretched arms in the opposite direction was noted.

The pertinent data are set forth in detail in the collection "Pervyye kosmicheskiye polety cheloveka" (First Space-Flights of Man), (1962), and in a number of papers by Soviet researchers (Yazdovskiy, Bryanov et al., 1963 Gazenko, Chernigovskiy, Yazdovskiy, 1964; Yuganov, Gorshkov et al., 1965; Kas'yan, Yazdovskiy, 1965; Kas'yan, Kolosov et al., 1966; Yemel'yanov et al., 1965).

All the disorders of motor coordination detected by various authors are usually accompanied by a redistribution of the muscle tonus and by changes in muscular bioelectrical activity. A.V. Lebedinskiy, Yu. G. Grigor'yev et al. (1964) emphasize that tonic reflexes, a most important part in the effectuation of which is played by the labyrinth, provide for the active posture of the body in its various positions and make it possible to move about under conditions of the constant action of gravity. It is only natural that with a change of the force of gravity, the specific nature of the tonic reflexes must also change. Realignment of the muscle tonus is a primary reaction of the organism in order to maintain the initial position of the parts of the body when gravitational forces are altered (Isakov, Yuganov, Kas'yan, 1964; Rosenblyum, 1963). Change of adjusting reflexes accompanying a change of gravity was observed by G.L. Komendantov, (1963), Gerathewohl and Stalling (1957). Yu. M. Yuganov, I.I. Kas'yan, N.N. Gurovskiy et al. (1961) detected decreased accuracy in muscular efforts during weightlessness in 14 test subjects. The effort applied in lifting a weight of 750 g was, on the average, excessive by 250-500 g; sometimes the error reached 1,250 g. Some changes of the tonus of the skeletal musculature were also observed by other authors, both during parabolic and orbital flights ("First Space-Flights of Man," 1962; Yuganov, 1965; Kas'yan, Kopayev, Yazdovskiy, 1965). Ye. M. Yuganov and I.I. Kas'yan, jointly with a number of other researchers (Yuganov, Kas'yan, Asyamolov, 1963; Gazenko, Kas'yan et al., 1964; Yuganov, Kas'yan et al., 1962; Yuganov, Kas'yan Yazdovskiy, 1960; Isakov,

Yuganov, Kas'yan, 1964; Kas'yan, Kopanev, Yuganov, 1964) conducted a series of studies on the bioelectric activity of the skeletal muscles under conditions of acceleration and weightlessness in rocket and airplane flights. The weightlessness lasted 25-30 sec or 5-6 min, the acceleration was 2 G or 6-7 G. Experiments were conducted on rabbits and cats. Muscular electrical activity was also studied in man. Biopotentials were recorded from straight ocular muscles (rabbits), from femoral muscles (dogs, man), from flexors and extensors of the forelimbs (cats) and from neck and dorsal muscles (man). When acceleration was /12
increased (up to 2.5-3 G), the amplitude of the biocurrents of the straight ocular muscles of mice increased 1.5-3 times. When acceleration was decreased, the value of biocurrents dropped to the baseline and sometimes below it. Acceleration caused downward deflection of the eyeball, while weightlessness caused upward deflection. The authors are of the opinion that under conditions of weightlessness, the labyrinthine tonic reflex of eye counter-rotation disappears. The amplitude of the biocurrents of extensor muscles also increased 1.5-2 times during acceleration, and decreased to the same extent in weightlessness. Almost the opposite pattern was observed with respect to flexor muscles: with acceleration the amplitude of the biocurrents either did not change or increased insignificantly, while in weightlessness it increased 1.5-2 times. Bioelectric activity of the neck muscles decreases under conditions of weightlessness. Sometimes even the phenomenon of "bioelectrical silence" is observed. However, the electric activity of the hand muscles increases approximately 3 times in weightlessness. The authors consider it possible to draw the conclusion that the muscle tonus (especially that of "antigravitational" muscles) decreases in weightlessness and increases during acceleration. This thesis is also confirmed by the results of experimental measurements of the muscular force of the arms for 26 persons under conditions of weightlessness: in 82% of cases the muscular force of the arms decreased by 4-22 kg. The authors did not comment on the apparently contradictory fact of the above-cited increase of electrical activity of hand muscles.

Similar results were obtained by Graveline et al (1961*) in experiments simulating partial weightlessness by immersion of the test subjects in water. After a 7-day immersion, the persons showed decreased muscular tonus and general lameness and weakness in the joints. However, these experiments are not faultless, since a number of factors besides partial weightlessness were also acting upon the test subjects.

* Cited by Ye. M. Yuganov and D.V. Afanas'yev, 1964.

The decrease of tonus and electrical activity can, nevertheless, not be regarded as the absolute and only reaction of the antigravitational muscles under conditions of weightlessness. Somewhat different effects are also mentioned in the literature. Thus, Grandpierre et al. (1962) observed an increase in weightlessness of the tonus of occipital muscles (on the basis of electromyographic data). During the orbital flight of the dogs Belka and Strekla the forces exerted by their paws were recorded by contact-potentiometer transducers. The movements of the dogs were recorded by two television cameras (Antipov, Bayevskiy, Gazenko et al. 1962). At the beginning of weightlessness, tension of all the muscles was observed. Later the rear paws developed continuous static tension; this firmly fixed the dog's position. /13

In the experiments with the monkeys Able and Baker on the Jupiter rocket, American researchers recorded the electromyogram of the sural muscle. Analysis of the electromyograms recorded during the flight does not disclose any symptoms of motor excitation or other deviations from the norm (Graybiel et al., 1959; Gerathewohl, 1960). However, the reliability of these results is doubtful because of too rigid and prolonged fixation of the animals in an uncomfortable posture (the monkeys were fixed face downward 64 hours before launching; nourishment was artificial, i.e., intraperitoneal); in addition, there were numerous problems with the equipment.

During the spaceflight of V.M. Komarov, K.P. Feoktistov, and B.B. Egorov on the "Voskhod" spacecraft, special investigations of the tonus of the ocular muscles were conducted with the aid of Herschel prisms. No significant changes in the tonus of the ocular muscles under flight conditions were detected (Yegorov, 1964).

Thus, the complex of factors in parabolic and orbital flights usually does not cause very strong changes in motor-coordination and mytonic reactions of the organism. However, some deviations in the distribution of muscular tonus and in the execution of motor acts (particularly fine ones) sometimes do appear, and under certain conditions may have serious consequences.

Besides the motor component, flight conditions sometimes cause the appearance of some other reactions, connected with changes of the functional state of the vestibular analyzer. Such are vestibular-sensory and vestibular-vegetative reactions.

In the state of weightlessness during aircraft flights along Keplerian trajectories, loss of spatial orientation is often observed (Clark et al., 1960; Gerathewohl and Stallings, 1959; Schock, 1961; Strughold, 1955). Roman et al., (1963) registered the appearance of visual and spatial illusions in 3 American officers during flight (during weightlessness) of the F-100 airplane.

Gerathewohl and Ward (1960) studied 47 test subjects. Of these 47 persons, 25 showed spatial disorientation in varying degree during weightlessness in Keplerian parabolic aircraft flight. The men expressed sensations of slow soaring, rising and falling, or of tumbling and hanging upside down.

L.N. Kitayev-Smyk (1964) investigated over 200 persons during parabolic flights; 92 of them had flight experience. During the period of weightlessness, 75% of those without flying experience had spatial illusions with the sensations of downward fall, turning over, etc.

Ye. M. Yuganov, I.A. Sidelnikov, et al. (1964) observed 30 test subjects during parabolic flights. They discovered /14 that with regard to the degree of expression of the vestibular-sensory reactions, the test subjects could be divided into three groups: the first group showed no ill effects during weightlessness; the second group experienced illusions concerning the position of the body; the third group rapidly developed airsickness with temporary loss of work capacity.

Development of vestibular-vegetative disorders similar to seasickness, and with typical symptoms of motion sickness, has also been observed by other authors (Komendantov and Kopanev, 1962; Schock, 1961; Johnson, 1961, et al). In the above-mentioned experiments by Gerathewohl and Ward (1960), besides sensory disorders the test subjects experienced slight reinforcement of respiration, slight vertigo and nausea, increased perspiration, fatigue, and sleepiness after flight. In some cases even more pronounced symptons of airsickness appeared: excessive perspiration, dryness in the throat, increase salivation, and a feeling of cold or heat. L.A. Kitayev-Smyk (1964) also indicated that, starting with the third to sixth period of weightlessness (with repetitions of a parabolic trajectory in flight), the test subjects experienced vegetative reactions (nausea, vomiting). The author found a relationship between the type of spatial illusions (sensation of turning over, ascending or falling) and the appearance of vegetative disorders. In persons without spatial illusions or with the illusions of falling, vegetative reactions did not occur or were very weak.

Some cosmonauts also experienced vestibular-sensory and vestibular or vegetative reactions during orbital flights in spaceships.

The changes were slight and did not decrease working capacity; however, they caused some inconvenience to the cosmonauts. During the transition to weightlessness many had transitory spatial illusions (Kas'yan, Kopanev, Yazdovskiy, 1964; McCutcheon et al., 1962; Augerson, Laughlin, 1961; Warren, 1963; David, 1963). Among the Soviet cosmonauts, illusions of being upside down were observed in the cases of G.S. Titov, P.R. Popovich, B.B.Yegorov, and K.P. Feoktistov (Yazdovskiy, Kas'yan, Kopanev, 1964; Yegorov, 1964; Yuganov, Gorshkov et al., 1965). The most marked shifts were observed in the case of G.S. Titov. All tests, applied before the flight (test for the duration of post-rotational nystagmus, for antirotational illusions, caloric test according to Voyachek, testing on Khilov's swing), testified to a normal functioning of the vestibular apparatus. He endured the accelerations very well. During the transition to weightlessness, a brief sensation of an overturned position of the body (upside down) suddenly appeared. Starting with the fourth orbit, symptoms resembling a slight degree of motion sickness appeared. Sharp turns and inclinations of the head caused vertigo and a sensation of the "floating" of objects coming into the field of vision. At the beginning of /15 the flight, the cosmonaut executed without difficulty a complex of four vestibular tests (worked out by I.I. Bryanov, F.D. Gorbov, and Yu. V. Krylov: test for muscular tonus of the arms, digital-nasal test, writing and figure drawing test, test for accumulation of Coriolis acceleration). There later appeared a feeling of heaviness in the head and the region of eyebrows, and a disagreeable sensation in the eyeballs when they were moved. When vestibular tests were repeated after 5 hours (and later 2 more times), vertigo was detected; in conducting tests involving the turning of the head, deflection of the extended arms appeared. The other tests were performed normally. The same phenomena of discomfort were also observed after sleep. Flickering of objects in the illuminator (optokinetic irritation) also caused disagreeable sensations. The described phenomenon disappeared from the moment of braking of the motion of the spaceship and the appearance of G-loads. Motor coordination was not disrupted during the entire flight.

After the descent and landing, and in the hospital, motor coordination, gait, and the accuracy of handwriting were normal. No spontaneous nystagmus or pathological reflexes were detected. All vestibular tests were executed easily and accurately. No disruptions of vestibular functions were detected later, several days and months after flight. The above material was taken from the book: "First Space Flights of Man" (1962) and from works of V.I. Yazdovskiy, I.I. Kas'yan, and V.I. Kopanev (1964); M.A. Gerd, N.N.Gurovskiy (1962); O.G. Gazenko, V.N. Chernigovskiy, V.I. Yazdovskiy (1964); Ye. M. Yuganov, A.I. Gorshkov (1964).

In the preliminary information given at the press conference about the results of the "Voskhod" spaceflight, B.B. Yegorov reported that during transition to weightlessness, he and K.P. Feoktistov experienced illusions of an overturned position (the one felt he was lying "face down," the other -- in a "head downward" position). During brisk motions of the head, slight vertigo and a general sensation of discomfort appeared. The indicated illusions experienced by B.B. Yegorov and K.P. Feoktistov appeared with closed and with open eyes, and remained for the duration of the flight up to the moment of braking of the craft.

The indicator and graphic tests showed a slight decrease of accuracy in executing fine coordinated motions. Work capacity was normal (Yuganov, Gorshkov et al., 1965). Special vestibular tests were successfully executed.

The corresponding reactions of American cosmonauts, according to available information, were generally similar to those of the Soviet cosmonauts (Augerson, Laughlin, 1961; Laughlin et al., 1962; McCutcheon et al., 1962; Medvedeff, 1962; Glenn, 1962; Clark, 1963; David, 1963; /16
Warren, 1963).

Transitory disorientation and spatial illusions were observed in the cases of Glenn, Cooper, Schirra, and others. An interesting case of distortion of visual perception and evaluation of space occurred in the case of G. Cooper: the cosmonaut asserts that he saw little houses and other objects on the Tibetan plateau during the flight (Warren, 1963).

In the origin of all the above-mentioned sensory and sympathetic reactions, an important role is evidently played by changed afferentation from the receptory zones of a number of analyzers, including the vestibular, proprioceptive, cutaneous, and other analyzers. Afferentation from the labyrinthine apparatus of the inner ear may be predominant against the background of changed pulsation. The vestibular apparatus is an ideal gravireceptor, which reacts very sensitively to changes in the direction and magnitude of the force of gravity. The threshold of its sensitivity is hundredths of "G". According to the data of Graybiel and Clark (Clark, Graybiel, 1961; Clark, 1963), the threshold for the perception of rotation is 0.12-0.17°/sec^2;

for linear accelerations the threshold value is 0.07 and for gravitational forces, 0.000344 G. The organ of equilibrium is strongly affected in all phases of spaceflight: ascent, orbital flight, and descent. The imporant role of the vestibular analyzer in the generation of motor disorders, disorientation, and the syndrome of the cosmic form of motion sickness is recognized by many researchers, Soviet and foreign (Gazenko, 1962; Parin, Gazenko, Yazdovskiy, 1962; Parin, Chernigovskiy, Yazdovskiy, 1960; Yuganov, Kas'yan et al., 1961; Yuganov, Kas'yan, Asyamolov, 1963; Yuganov, Afanas'yev, 1964; Yuganov, Gorshkov et al., 1965; Kas'yan, Kopanev, Yazdovskiy, 1957; Kas'yan, Kolosov et al., 1966; Yazdovskiy, Yemel'yanov et al., 1965; Clark et al., 1960; Clark, 1963; Gerathewohl, Ward 1960; Graybiel, Johnson, 1963; Lomonaco et al., 1957; Fiorica et al., 1962; Mazza, 1963; and others).In this connection, the data cited in an article by Yu. M. Volynkin and P.P. Saksonov (1965) are of considerable interest. According to this article, the more highly an animal is organized, the less disrupted is the coordination of its movements during parabolic and orbital flights. In monkeys and in humans, visual correction acquires great importance. In rodents, however,where the specific importance of the vestibular apparatus in physiological functions is very great, stronger disruptions of motion coordination occur.

The investigations of Ye. M. Yuganov, I.A. Sidel'nikov and others show a strikingly clear relationship in the test subjects, between the degree of expression of sensory reactions in parabolic flights and the degree of functional stability of their vestibular analyzer, as determined by a complex of laboratory tests. Differing sensitivity /17
of the vestibular analyzers determined differing tolerance to weightlessness.

The responsibility of the vestibular analyzer for the appearance of motor-coordination disorders and some sensory and vegetative disorders is also confirmed by many experiments with labyrinthectomy. In the above-quoted works of Ye. M. Yuganov et al., on the study of muscular tonus in connection with changed gravitation, labyrinthectomy of animals resulted in the decrease of shifts as compared to intact specimens. The amplitude of biocurrents of flexors and extensors in weightlessness remained almost unchanged (Yuganov, Kas'yan, Asyamolov, 1963; Gazenko, Kas'yan, et al., 1964).

It was subsequently established (Yuganov, Afanasyev, 1964) that the lessened expression of disorders appears only after an acute period of labyrinthectomy (3-4 days).

After compensation of motion disorders resulting from labyrinthectomy, rats and mice in a state of weightlessness did not revolve, but "floated" calmly.

The amount of artificial gravity necessary for the prevention of changes is considerably smaller for such animals, than for intact animals. Howeer, during the acute period of labyrinthectomy, tolerance of these animals to weightlessness was worse than that of intact specimens.

Lomonaco et al. (1957) discovered in the above-mentioned "Roman tower" that the movements of deaf-mutes (5 persons) became less uncoordinated than those of normal subjects. Basically the same results were also obtained by S.S. Makaryan (1966) in determination of the sensitivity of deaf-mutes to the action of accelerations of various kinds. Persons with affected labyrinthine function did not have illusory sensations or vertigo, and the motion sickness syndrome did not develop.

In an American rocket flown at an altitude of 236,000 feet, a labyrinthectomized mouse did not show any agitation during weightlessness. Intact mice revolved and showed symptons of agitation (Hanrahan, Buschnell, 1960).

Of special interest to us are the experiments of Beckh (1954) and Schock (1961). These researchers disconnected in turtles and cats not the entire vestibular apparatus, but only the otoliths. Experiments were also conducted with cutting of the eighth pair of cranial nerves or removal of the cortical part of the vestibular analyzer (in cats). Animals whose labyrinthine cortex had been removed had lesser disruptions of orientation in a state of weightlessness during parabolic flights than did intact animals. Animals with disconnected otoliths did not show any visible changes, but with eyes closed acute disorders appeared. The observation of Hasegava (1949, 1955) has basically the same significance. /18
He established that man becomes more resistant to motion sickness (under terrestial conditions) when his otoliths are dissolved. Intravenous injection of 3-4 ml 5% soda solution in rats dissolved the otoliths and had a prophylactic effect. Such animals were quiet in weightlessness, their coordination was less distorted, they did not revolve, but crawled on the walls of the container (Gazenko, Kas'yan et al., 1964). This method may be of importance for preventive treatment of sicknesses connected with disorders of the otolithic function. The results give some ground for the assumption that space-flight factors (at least the dynamic ones) have a particularly strong effect on the otolithic part of the vestibular apparatus. The role of otoliths as the basic specific gravireceptor is generally

recognized. The otoliths perceive pressure and traction, changes in motion and linear acceleration, and take part in the formation and course of motor acts (Gerd, Gurovskiy, 1963; Gerathewohl, Ward, 1960; Sasaki, et al., 1963). Phylogenetically, this system is older and more closely connected with conditions of terrestial gravitation. Schöne (1964) proves that the perception of spatial position is determined exclusively by the activity of statoliths and is subject to the influence of other receptors. It may also be regarded as generally recognized that the otolithic apparatus plays a leading role in those deviations from the usual state which take place in motor and sensory reactions under conditions of weightlessness (Gerd, Gurovskiy, 1962; Yazdovskiy, Kas'yan, Kopanev, 1964; Johnson, 1964; Brown, 1961). All researchers recognize that space flight factors create unusual conditions for the functioning of the receptors of a number of afferent systems, including first of all the otoliths. Cutaneous and proprioceptive sensitivity decreases, and changes occur in afferentation from the otholithic apparatus, and in the volume of afferent impulsation as a whole, thus leading to the disruption of spatial analysis (Gazenko, 1962).

The opinions of scientists differ somewhat only concerning the character of the changed pulsation from the otoliths in a state of weightlessnes. Or, rather, concerning the presence or absence of such pulasion. Some scientists are of the opinion that the most evident and most probable effect of weightlessness is, in this respect, the unique deafferentation of otolithic apparatus. The otolith of the utriculus does not function during weightlessness, since the zone of the receptors connected with the gravitational field of the Earth ceases to function. Therefore the otoliths exert a lesser inhibiting action (or no action at all) on the excitability of the semicircular canals. Reciprocally, the excitability of the cupulo-endolymphatic apparatus is increased, afferentation from the semicircular canals of the labyrinth becomes relatively predominant. /19
Then irritations in the case of head movements become greater than threshold, and cause sensory and vegetative shifts. Sensitivity to Coriolis accelerations increases sharply. Under natural conditions, accelerations are transitory ans are accompanied by increased tonus of otolithic apparatus which inhibits the reactions of semicircular canals. In spaceflight the inhibiting action of the otoliths is limited by weightlessness, while the accelerations are great and protracted. The irritations are cumulative; this in time leads to development of the space motion sickness syndrome (Gazenko, 1962; Kas'yan, Kopanev, Yazdovskiy, 1964; Komendantov, Kopanev, 1962; Lebedinskiy, Grigor'yev, et al., 1964; Parin, Chernigovskiy, Yazdovskiy, 1960; Roman, 1963; King, 1961; Johnson, 1961; Johnson, Taylor, 1961). Precisely the prolapse of the functions of the utriculus

explains the absence of compensatory motions of the head ~~in~~ pigeons during inclinations to the left and right in flights in the C-131 airplane (King, 1961).

Other authors, however, do not regard it as possible to speak of functional exclusion of otoliths in weightlessness. Pulsation from the otolithic apparatus does not cease, but changes qualitatively. Of importance are not so much the magnitudes of accelerations under conditions of spaceflight, as their form. Changed irritants are addressed to the otoliths, and cause the qualitatively different responses (Gerd, Gurovskiy, 1962; Yazdovskiy, Kas'yan, Kopanev, 1964; Yuganov, 1965; Clark et al., 1960). This conception is developed in greatest detail in the works of Ye. M. Yuganov and A.I. Gorshkov (1964) and V.I. Yazdovskiy and M.D. Yemelyanov (1964). Ye. M. Yuganov and A.I. Gorshkov (1964), and Ye. M. Yuganov (1965), have investigated the excitability of the vestibular analyzer in man (14 subjects) under conditions of short-term weightlessness. The possible trace effect of previous accelerations was controlled by the authors in experiments on a centrifuge. Not an increase, but a decrease of the excitability of receptor formations of the semicircular canals to angular accelerations and to Coriolis accelerations was established on the basis of a whole series of tests. The authors consider that this decrease of excitability cannot result from the direct action of weightlessness on the semicircular canals, since the loss of weight of the endolymph and the cupula does not mean the loss of mass, and does not lead to alteration of the inertia of the endolymphatic fluid. They assume that this phenomenon is determined by change of the reciprocal relations between the semicircular canals and the otolithic apparatus. Pulsation from the otoliths in weightlessness exerts greater inhibiting action on the semicircular canals than it does under ground conditions. In weightlessness the otoliths, according to these authors, serve as the source of unusual, enhanced afferentation. Weightlessness does not lead to deactivation of the otolithic apparatus, but is for it an unusual irritant which causes excitation of the receptor formations of the otolithic part of the vestibular analyzer. In this connection, weightlessness should be evaluated as a "minus-irritant" /20 (the agent is an irritant even when its intensity is decreased). This irritant is characterized by special features in the origin and course of qualitatively new vestibular-sensory and vestibular-vegetative reactions, and by uniqueness in the interrelationships between the otoliths and the cupular parts of the analyzer. Weightlessness is a special irritant which does not affect man in the process of ontogenesis and phylogenesis. As every irritant, the zero-G state has as a property the cumulation of the effects of its action. Summation of the processes so generated in the cortical-subcortical formations may lead to the appearance of symptoms of motion sickness.

Comparing the literature data, V.I. Yazdovskiy and M.D. Yemel'yanov(1964) also concluded that the otoliths continue to function in weightlessness. There are grounds for believing that weightlessness and the state of delabyrinthization (deactivation of the otoliths) cause phenomena of a different order. Moreover, the hypothesis of the cumulative effect of Coriolis accelerations on the stimulated semicircular canals cannot be sustained, since the velocities of rotation of the "Vostock" spaceships lay beyond the thresholds of sensitivity. The authors also point out that centrifugal forces, rectilinear accelerations and their combinations, acting in space flight, must shift the otoliths, and all shifting is a form of neural-cell irritation.

The decrease of excitability of the semicircular canals during weightlessness is noted also in the work of P.K. Isakov, Ye. M. Yuganov and I.I. Kas'yan (1964). During flights along a Keplerian trajectory, Roman et al. (1963) did not detect in humans (3 USA officers) any quantitative difference in the responses of semicircular canals during normal or zero gravity. The authors are of the opinion that the activity of the cupulo-endolymphatic system does not undergo considerable changes during the period of weightlessness. Thus the establishment, by several researchers, of the absence of increase, and on the contrary, even of the decrease of excitability of the semicircular canals in weightlessness is indirect proof that the otoliths continue to function even under zero gravity.

Another indirect proof of this fact are all the above-mentioned experiments by Beck (1954), Schock (1961), and Hasegava (1949, 1955) with deactivation of the otoliths. Experimental deactivation of the otolithic part of the labyrinths, with its functional differentiation in weightlessness, could no longer affect the severity of motor, vestibular-sensory and vestibular-vegetative disorders. The reactions of such animals during weightlessness would not differ from the corresponding reactions of intact animals. /21

Above we have already cited the work of Ye. M. Yuganov, I.A. Sidel'nikov et al. (1964), where a relationship was established between the degree of sensory and vegetative reactions in weightlessness and the functional stability of the vestibular analyzer. It is interesting to note that this relationship was not detected in tests causing the irritation of semicircular canals (for example, the rotary test, the test with double rotation), but was very clearly visible in those tests which determined the activity of the otoliths and the interaction between the vestibular apparatus and other analyzers (the test for cumulation of the effects of Coriolis accelerations, the test on Khilov's swing, the test with an unstable support, and the test for inhibition from proprioceptors). The authors do not stress it, but the fact itself evidently demonstrates that the appearance of sensory and vegetative deviations occurs with the participation of the otoliths and, basically, not via the semicircular canals. Finally, B.B. Yegorov (1964), speaking about the discomforts during the flight of "Voshkod" spaceship, points out that there was no involuntary motion of eyes, as with irritation of the semicircular canals. Sensation of rotation was not observed either; no connection could be established between the occurring changes and the movements of the ship. Subsequent analysis of the results of the flight fully confirmed the conclusions about the absence of connection between the apperance of illusions or the syndrome of motion sickness and the symptoms of disturbance of the functions of the cupular system (Voskresenskiy, Gazenko et al., 1965; Yuganov, Gorshkov et al., 1965). These preliminary conclusions apparently testify to the absence of increased excitability of the semi-circular canals during weightlessness, and to the fact that the Coriolis accelerations connected with motion of the ship do not have pre-eminent importance on the genesis of the observed changes.

At present, the majority of Soviet researchers connect the origin of motion sickness and possible motor disorders with the so-called disturbance of functional systematization in the work of the analyzers of spatial relations (the formulation was given by G.I. Komendantov and V.I. Kopanev, 1965). A.V. Lebedinskiy, Yu. G. Grigoryev et al. (1964) point out that for the vestibular analyzer, the role of inductive relations with other analyzers is particularly important. Because of the constant action of gravity, the position analyzer has not,in the process of phylogenesis, developed those mechanisms which limit the flow of irritant (as, for instance, eyelid, pupil, tensor tympani, etc.). The functional state of many afferent systems changes under the influence of a complex of unusual factors during spaceflight. For example, in weightlessness a number of reactions appears resulting from the decrease of body weight: change of muscle tonus and of afferentation from proprioceptive, interopceptive, visual, cutaneomotor and /22
other analyzers. Besides this direct influence of weightlessness, its intermediary effect appears as the disruption of coordination in the work of the analyzers. Different reflector interrelations than those on Earth

originate among the afferent systems and analyzers participating in the formtion of spatial concepts. It has been experimentally established thatthe sensitivity thresholds of the vestibular apparatus and the thresholds of motor and sensory vestibular reactions are substantially affected by the character of muscular activity (proprioceptive afferentation), the presence of the absence of visual control, and the state of the motor analyzer. Relations conducive to the lowering of sensitivity thresholds of the vestibular analyzer and the strengthening of specific reactions can originate under conditions of space flight (Gualtierotti, Margaria, 1964). The degree and character of interaction among analyzers changes, as do also the reaction threshold of each individual analyzer. Functional shifts appear also in a number of subcortical formations, in the cerebellum and in other structures, ensuring statokinetic stability. All these circumstances may be conducive to the development of the cosmic form of motion sickness. Many propositions of this theory still lack direct proof, and a number of problems require further investigation (Komendantov, Kopanev, 1962; Yazdovskiy, Yemel'yanov, 1964; Lebedinskiy et al., 1964; Kas'yan, Kopanev, Yazdovskiy, 1964; Parin, Chernigovskiy, Yazdovskiy, 1960; Yazdovskiy, Yemel'yanov, Gurovskiy, 1962; Yemel'yanov, Yuganov, 1962; Collec. "Pervyye Kosmicheskiye polety cheloveka",1962).

Experimental investigations also confirm the participation of other vestibular shifts of an entire series of neural formations in the pathogenesis of spatial motion sickness. G.V. Altukhov and V.I. Kopanev have investigated the effect of statokinetic irritants (Yarotskiy test, Barani rotation, Coriolis acceleration) on the bioelectric activity of the cerebral cortex and a number of othr physiological parameters. They have detected change in the amplitude of EEG (electroencephalographic) potentials (differently for different rhythms and different persons - variability of the force of basic neural processes) and a decrease in the values of the indicator of functional capacity of the cortex. It is interesting to note that the same directionality of EEG shifts in the frontal and in the temporal region of the cerebrum was very often observed. The authors note the similarity of the observed changes with electrophysiological phenomena accompanying motion sickness. A decrease of excitability and the development of inhibition in higher regions of the cerebrum also takes place. In persons with stronger resistance to vestibular irritations, bioelectric activity and indicators of the functional capacity of the cerebral cortex increased. L.A. Kitayev-Smyk (1963) also observed diffuse inhibition /23 in the corresponding centers of the cerebral cortex with change in the level of proprioceptive afferentation in parabolic flights.

During the flight of the "Veronica" ballistic missile, Grandpierre, et al.(1962) recorded the biocurrents from the field of vision and from the centers of proprioceptive sensitivity of the cerebral cortex of rats. During the entire flight of the missile, cortical bioelectric activity increased. Slow waves were observed in weightlessness. The authors speak of an increase of cortical excitability during accelerations and during recovery from them. The possibility of disruptions in the activity of the central nervous system, and of change of its functional properties and reactivity under the influence of spaceflight factors, are noted also in other sources (Collect. Pervyye kosmicheskiye polety cheloveka," 1962; Mallan, 1956; Hauty, 1960; and others).

The tests involving labyrinthectomy can also be explained from the point of view of the concept concerning disturbance of the functional systematization of analyzers. During parabolic and orbital flights, the greatest disturbances in the various analyzers evidently occur in the vestibular apparatus, basically in its otolithic part. A greatly changed pulsation flows from the otoliths, thus worsening the conditions for the appearance of a new systematization more adapted to the conditions of weightlessness. Thus, under these conditions the pulsation from the vestibular apparatus becomes quasi-superfluous, and contributes to the development of disturbances. In connection therewith, in case of labyrinthectomy vestibular disturbances decrease, and a smaller artificial gravity is necessary for normalization of the organism's functions (Yuganov, Afanas'yev, 1964; Yazdovskiy, Kas'yan, Kopanev, 1964; Gazenko, Kas'yan et al., 1964).

The formation of a new systemtization in the work of analyzers, corresponding to the changed conditions, is determined by the development of adaptation. A fairly rapid development of adaptational-compensatory reactions in recurrent or prolonged effects of flight factors is noted almost by all researchers (Yazdovskiy, Kas'yan, Kopanev, 1964; Geranthewohl, Ward, 1960; and many others). It has been established that the adaptational compensatory mechanism of vestibular disorders is in many respects determined by the character of visual perceptions, proprioceptive pulsation, and afferentation from a number of other analyzers (Yemel'yanov, Yuganov, 1962; Gerathewohl, Stallings, 1957; Yazdovskiy, Kas'yan, Kopanev, 1964, and others). A large role also belongs to the processes of central adaptation

(Altukhov, Kopanev, 1964), whose particular importance for the functions of vestibular analyzers is stressed by A.V. Lebedinskiy, Yu. B. Grogoryev, and others (1964).

The phenomena of adaptation and compensation take place for all types of disturbances connected with change of the vestibular functions. In case of prolonged or recurrent weightlessness, the motor-coordination disturbances start to decrease gradually. The rotation of animals around the longitudinal axis of the body ceases (Antipov, Bayevskiy et al., 1962; Yazdovskiy, Yuganov, Kas'yan, 1960; Volynkin, Saksonov, 1964); the accuracy of muscular efforts and of finely coordinated motions in people increases (Yuganov, Kas'yan, et al., 1964; Gerathewohl, Stallings, 1957; Lomonaco et al., 1957), etc. As a result of adaptational processes, vestibular-sensory and vestibular-vegetative shifts slacken or entirely disappear. Correct spatial orientation is restored and sometimes the symptoms of motion sickness are eliminated (Yegorov, 1964; Kitayev-Smyk, 1964; Komendantov, 1962; Collec. Pervyye kosmicheskiye polety cheloveka," 1962; Clarke et al., 1960; Brown, 1961; Henry, Ballinger, et al., 1952; Strughold, 1955). /24

However, certain data indicate that in some cases adaptation may not materialize (Yazdovskiy, Yuganov, Kas'yan, 1960; Kas'yan, Kopanev, Yazdovskiy, 1964; Beckh, 1954). Moreover, the new systematization in the work of analyzers appears to be less stable than the old, and under adverse conditions may be disrupted. In this connection, training of the vestibular apparatus, with account taken of functional systematization in the work of the analyzers of spatial relations, becomes of great importance (Kas'yan, Kopanev, Yazdovskiy, 1964; Lansberg, 1965). The dependence of vestibular manifestations on visual irritations, muscular efforts, and other factors must be taken into account here (Yemel'yanov, Kuznetsov, 1962; Yuganov, Markaryan, Bryanov, et al., 1963; Gurovskiy, Yemel'yanov, Karpov, 1965). With the aid of a system of such training it was possible to increase the resistance of our cosmonauts to vestibular irritations under flight conditions (Yasdovskiy, Yemel'yanov, 1964; Gazenko, Chernigovskiy, Yazdovskiy, 1964).

However, there remains an urgent task of further investigating the effect of individual space flight factors, as well as of the entire complex, on the vestibular analyzer and on the entire system of analyzers controlling the perception of space. The problem has many unsolved questions of great importance to cosmonauts (Yazdovskiy, Yemel'yanov, 1964; Parin, Chernigovskiy, Yazdovskiy, 1960; Sisakyan, 1961).

It must be noted that until recently, investigation of the functions of the vestibular analyzer has basically had a purely applied, clinical character. Experimental works on the study of the problem of how vestibular functions are affected by these or those factors occurring in the spaceflight, so far have been very few and sometimes contradictory.

Effect of Accelerations During Centrifugation on the Functional State of the Vestibular Analyzer /25

The perception of gravity is a specific function of the vestibular analyzer. Thus, it is natural to expect that accelerations will substantially affect particularly this system; this was confirmed by experiments in flight. Purposeful laboratory investigation of this problem was begun only in the past several years; the results of such investigation are so far incomplete and contradictory.

Morphological and histochemical investigations have detected, as the effect of accelerations, a number of gross disruptions and finer structural changes in the region of the inner ear. Magnus (1924) used short-term but rapid centrifugation (2000 rpm) for deactivation of the otoliths. The otolithic membrane was torn off the neural epithelium of the macula. Hemmorhages in the labyrinth were observed. R. Ye. Kogan and S.S. Markaryan (1963) have detected, in the innder and middle ear of a dog, hemmorhages of various degrees after exposure to accelerations from 2.4 to 14.5 G in the head-trunk and trunk-head direction. Most often, the hemorrhages occurred in the perilymphatic space of the cochlea and in the sacculus. Finer and more directional changes in the structural and cytochemical organization of the capillary cells and synapses of the utriculus were detected by Ya. A. Vinnikov, O.G. Gazenko et al., (1963) after the action of radial accelerations (1.5; 3; 10 G) in the dorsum-thorax direction. The authors have investigated the utriculus of guinea pigs, cats, monkeys, and pigeons at different intervals after rotation. Along with some typical generic peculiarities, there were observed specific shifts common for all types of animals. Accelerations of 10 G during 3 minutes lead to a redistribution of ribonucleic acids (RNA) in the nucleus amd cystoplasm of capillary cells and neurons of the vestibular ganglion. Lumps of RNA in the cystoplasm disappear, the nuclei swell, the nucleoli are ejected and settle under the nucleus. With time, the nucleoli disintegrate and form specific sections of the endolymphatic networks where protein-synthesis processes later take place intensively. A new nucleolus is formed in the center of the nucleus. The amount of total protein and of its functional groups decreases considerably, with a subsequent increase during the restorative period. Changes occur in the activity of enzymes, and in the content and localization of mucopolysaccharides. The authors are of the opinion that the observed changes characterize the state of excitation in the receptor structures of the utriculus. The huge physiological load during accelerations causes considerable expenditure of proteins and nucleic acids in the cystoplasm. Ejection of the nucleolus is a compensatory act of the transmission of m-RNA from the nucleus to the plasma, and helps to preserve the functions of utricular cells. Thus, the precise mechanism of utricular functions is connected, in the authors' opinion, with the redistribution of nucleic acids, processes of /26 protein synthesis, with participation of the cholinenergic mediator system of the tissues. Some studies with the application of special functional tests also detect an increase in the excitability of the vestibular apparatus after the action of accelerations.

Winget, Smith, and Kelly (1962) subjected chicks to prolonged centrifugation (35 and 49 days) with accelerations from 1.5 to 2 G. On the basis of changes in the direction of the postnystagmus and othe cupulometric parameters, an increase of labyrinthine sensitivity in birds after centrifugation was established. The rise of the excitability of the vestibular apparatus was also noted by V.A. Shabalin (1961), when people were subjected to the action ofa periodical angular movements (accelerations up to 2 G). Cramer et al. (1963) recorded the electronystagmograms of cats during optokinetic irritation after stimulating the labyrinth (horizontal semicircular canals) by angular velocities of a particular magnitude (0.1-0.4 rad/sec^2). The action applied changed the dynamic characteristic and amplitude of responses to a series of experimental vestibular irritations.

Change of the character of nystagmic reactions with different magnitudes of rotational accelerations and G-forces were observed by Evans et al. (1962). The authors recorded the movements of the labyrinthine cupula, action potentials of the vestibular nerve, nystagmic movements of the eyes, and accelerometric and chronometric data. A.Ye. Kurashvili (1962) detected in dogs an increase of the vestibular reactions during 15 minutes rotation on a centrifuge. The effect of accelrations on the functional state of the vestibular analyzer is confirmed also by the appearance, in some cases, of difficulties in the spatial orientation of test subjects exposed to accelerations over 3 G (Shubert, Kolder, 1962; Whitside, 1961; Graybiel, Clark, 1962). Illusions of shift of the visual target upwards (oculogravic illusion, according Graybiel) occur, adequate perception of the vertical and horizontal is disrupted, etc.

During accelerations, particularly in test subjects with increased vestibular sensitivity, various vestibular vegetative disorders also appear: weakness, fever, excessive perspiration, vertigo, nausea (Markaryan, 1963). Phenomena of motion sickness under prolonged rotation (with accelerations of only 0.1 G, but Coriolis accelerations were also present) were also observed in monkeys (Meek, Graybiel et al., 1962). Disapperance of the vegetative components of the effect of accelerations in larynthectomized animals (Kurashvili, 1962) testifies to the participation, in their genesis, of irritation of the receptors of the vestibular apparatus /27
by the changed gravity field.

Under the action of accelerations, motion-coordination disruptions also often appear, connected with change of the functional state not only of the motor analyzer, but also of the vestibular analyzer. At the moment of influence of the accelerations and thereafter, coordination of motions and the stability of body equilibrium became disrupted (Makaryan, 1963). In an increased gravity field (0.3-2 G), a slight increase of the amplitude of body swaying in standing men was noted (Garfinkel, Isakov et al., 1959). During action of accelerations (3-7 G), differentiation of required pressures exerted on a lever worsened (Chkhaidze, 1962). In rats after 50-day centrifugation of 5 minutes each day (10, 15, and 20 G), the motor reflex of pressure on a lever was disrupted, the accuracy and the number of pressings decreased. During small accelerations (2-5 G), the behavior of rats did not change (Herrick, 1961). During and after prolonged centrifugation (1.5-2 G during 35 and 49 days), postural and locomotor abnormalities often appeared in chicks (Winget, Smith, Kelly, 1962).

Margaria and Gualtierotti (1962) observed equilibrium disruption of sitting frogs and swimming fish after 10-minute action of large accelerations (2000 G). Percussive and rapidly changing accelerations of great magnitude (24-450 G) were accompanied in monkeys by phenomena of uncoordination with involuntary motions of extremities and trunk, and by tremor. The same phenomena were also observed with large accelerations (20G) in people (Bruce, Barr, 1963; Rhein, Taylor, 1963).

The bioelectric activity of skeletal muscles (particularly extensors of the extremities, respiratory muscles) was increased during accelerations. The amplitude of muscular currents usually increase with the increase of accelerations up to 4-5 G; with larger magnitudes, no further increase of muscular electric activity could be observed. During prolonged action of accelerations, the maximum value of myoelectric activity took place at the beginning of the plateau; later the amplitude of biocurrents gradually decreased (Babushkin, Isakov, et al., 1961; Kotovskaya, Lobashkov et al., 1962; Marukhanyan, Isakov, et al., 1962; Barer, 1962; Barer, Golov et al., 1963; Rhein, Taylor, 1963). It may be regarded as established (Babushkin, Isakov et al., 1961) that the increase of bioelectric activity of muscles testifies to increase of the tonus of muscles. In the opinion of many researchers, the tonus of the skeletal muscles is an important compensatory mechanism under the action of accelerations. Change of the tonic tension of muscles facilitates the performance of many vitally important processes (motor function, blood circulation, respiration), and increases the stability of the organism to accelerations (Barer, Golov et al., 1963; Babushkin, Isakov et al., 1961; Barer, 1962 a and b). Pulsation /28 from the vestibular apparatus plays an important role in the realization of protective myotonic reflexes during accelerations (Rosenblum, 1963; Yuganov, Kas'yan, Asyamolov et al., 1963).

During the first phase of the reaction of the organism to the action of accelerations (Barer, 1960 a and b; Rosenblum, 1963) - the phase of relative compensation - the regime of work of the nerve center changes: there occurs switching-in of a complex of adaptational-compensatory systems whose excitation inductively inhibits a number of other functions, less important at the given moment. Switching-on of the central mechanisms into the reaction of the organism to accelerations is confirmed by the change of the functional state of the cerebral cortex. The state of conditioned-reflex activity and electroencephalographic recordings testify to the fact that at the beginning of the action of accelerations, the force and mobility of neural processes of the functional systems of the cerebrum is increased. The processes of excitation predominate. Then symptoms of overtension appear, and inhibiting processes begin to prevail. Deep inhibition gradually develops in the cerebral cortex. Small accelerations cause excitation processes in the cortex; during large accelerations an inhibitory state develops very rapidly. The correlation of the basic nervous processes in the cortex and subcortex changes (Izosimov, Razumeyev 1962 a and b; Barer, Golov et al., 1963; Belay, Vasil'yev, Kolchin, 1964; Kislyakov, 1958; Barer, 1962 a and b; Savin, Sulimo-Samuylo, 1960).

Here, on the background of general inhibition, potent foci of excitation are created in the cortex and, possibly, in other sections. One such focus is localized in the region of the motor analyzer (Medvedev, 1963). The system vestibular analyzer-antigravitational muscles is apparently also one of the protective-compensatory systems under the action of overloads, as is indicated by all the abovementioned changes in the non-auditory labyrinth. Electroencephalograms of the deeply seated structures of the temporal region and the brainstem reflect the propagation of spasmodic discharges at the moment of the action of accelerations and afterwards (Adey, French et al., 1961). During centrifugation, the bioelectric activity of cerebellum, which is functional connected with the vestibular-motor system, is also enhanced. (Gualtierotti, Schreiber et al., 1959).

The problem of adaptation of the organism to accelerations is very complicated. During prolonged or repeated accelerations, depending on many circumstances, adaptation to the action of accelerations (Klimovitskiy, 1964 a; Usachev, 1961; Kislayakov, 1956, and others) was observed, as well as the absence of adaptation and even the cumulation of effects. With respect to the reactions of the vestibular apparatus, there are also indications of adaptive phenomena (Markaryan, 1963; Dmitriyev, Kotova, 1960: Lauver, 1961; Lawton, 1962) and of the summation of acceleration effects (Kurashvili, /29
1962; Gualtierotti, Schreiber et al., 1959).

All the above-described physiological investigations demonstrate the influence of accelerations either on labyrinthine functions in general, or, most often, on the functions of the semicircular canals. Singularities in recording of the response reactions and of the test probes used provided for study of the cupular part of vestibular apparatus. No special investigations of the effect of accelerations on the otolithic part of the labyrinth have been found in the accessible literature. However, some known facts point out its sensitivity to the action of accelerations. Such is the fact that the nystagmic reaction of persons exposed to the action of angular accelerations of various magnitudes depends on the body posture relative to the vertical axis of rotation (Markaryan, 1963). The dependence of information from otoliths upon the direction of radial acceleration (2.5-3G) was discovered by Schubert and Kolder (1962). In the above-mentioned work of Ye. M. Yuganov, I.I. Kas'yan, and B.F. Asyamolov (1963), change of the muscle tonus during accelerations is evaluated as a consequence of effects from the vestibular analyzer. Considering moreover, that vestibulotonic effects on the extensor muscles originate from the utriculi (Magnus, 1924), the participation of otoliths in the change of the level of muscular electro-activity during accelerations appears entirely possible. The active reaction of otolithic receptors to accelerations is also confirmed by the above-described histochemical investigations.

However, the specific character of the activity of the otoliths under conditions of accelerations has not yet been sufficiently studied; for quantitative investigations, special experiments must be carried out, with the use of strictly dosed testing irritation of these receptors of the vestibular apparatus.

Effect of Vibration on the Functions of the Vestibular Analyzer

Vibration has many-sided effects on the organism; it is an irritant of the receptors of all organs and tissues (Andreyeva-Galanina, 1963, Borshchevskiy, Yemel'yanov et al., 1963). Most researchers consider that there is an independent type of vibrational sensitivity with extensive cortical representation. It is asssumed that specific vibroreceptors are located in numerous tissues of the body, particularly in the skin and in the kinesthetic apparatus (Andreyeva-Galanina, 1956; Borschevskiy, Yemel'yanov et al., 1963; Donskaya, Stoma, 1960, and others). In addition, many authors indicate also the particular importance of the vestibular analyzer in the perception of vibration, which can be a strong adequate or inadequate irritant of the equilibrium organ (Voyachek, 1946; Kulikovskiy, 1939; Yazykov, 1951; Usenko, 1961; Kostrov, 1958; Krizhanskaya, 1949; Shpil'berg, 1960, 1962; Ernsthousen, 1950). It is /30 thought that the otolith of the saccule has specific sensitivity to vibration irritants (Kostrov, 1958; Usenko, 1961; Yazykov, 1951). However, in case of low-frequency vibration, rotatory motion of the head along an ellipsoid takes place, i.e., there is angular velocity and acceleration, consequently irritation takes place not only in the otoliths, but also in the semicircular canals of the labyrinth. Vibration with frequencies of up to 16-20 cps is regarded as an adequate irritant of the vestibular apparatus. Higher frequencies apparently act on the labyrinth as already inadequate irritants (Usenko, 1961; Andreyeva-Galanina, 1963). The labyrinth is very sensitive to vibrations, functionally as well as morphologically. True, morphological changes during strong vibration occur more often in the auditory part, but shifts are also noted in the non-auditory labyrinth. After vibration, histochemical investigations show degenerative and atrophic changes in the vestibular ganglia and in the capillary cells of the ampular crests and the otolith membranes. Hyperemia and other symptoms of receptor irritation appear (Popov, 1940; Temkin, 1960).

Despite the particular importance of the vestibular analyzer for the perception of vibration, very few special physiological investigations of the effect of vibration on the functional state of that organ have been made. For a long time, the effect of vibration on the organism was considered from the point of view of professional pathology. But even such clinical studies have noted an entire series of symptoms connected with disturbances of vestibular functions. Persons exposed to the action of industrial vibrations often experience vertigo, nausea, spontaneous nystagmus, and other discomfort phenomena (Saltykovskiy, 1927; Lebedeva, Tsuy Chahun-syan, 1960; Labadze, Khvatasi, 1963; Drogichina, Metlina, 1962; Artamonova, Zuyev, Khaymovich, 1963; Butovskaya, Agashin, 1957; Markaryan, 1959; Butkovskaya, 1959; Andreyeva-Galanina, Lebedeva, 1955; Braylovskiy, 1927; Caterson, A.D. et al., 1962; Gormann, R., 1940; Loeckle, 1950; Bugard, Souvras, 1953).

In some cases sensations appeared of objects flickering and rotating before the eyes, dazzling, or sensations of falling down, or visual and auditory halluncinations (Andrianov, 1960; Kublanova, 1960). A tendency towards increased arterial pressure and increased pulse frequency was noted (Lebedev, Tsuy Chzhum-syan, 1960). Many authors point directly to a connection of such reactions with the functional state of the vestibular analyzer (Mikulinskiy, 1963; Borshchevskiy, Koreshkov et al, 1958; Butkovskaya, 1959; Andreyeva-Galanina, Lebedeva, 1955; Lebedeva, Tsuy Chzhu-syan, 1960; Bugard, Souvras, 1953).

Among the motor-coordination disorders appearing /31 particularly often under the action of vibration are tremor of eyelids and fingers, increase of the amplitude of trunk swaying, disruption of equilibrium, instability in Romberg's position (Vozhzhova, Lebedeva, 1960; Braylovskiy, 1927; Butkovskaya, Agashin 1957, Artamonova, Mikulinskiy, 1963; Sirotina, Kharicheva, 1959; Artamonova, Zuyev, Khaymovich, 1963; Krizhanskaya, 1949; Lebedeva, 1963; Terent'yev, 1958, and others.

In the complex of investigations conducted by I. Ya. Borshchevskiy, M.D. Yemel'yanov, et al. (1963), disruption of static and dynamic coordination of motions during and after vibration was detected. The increase of the latent period,and of the time spent on the execution of a given motion, was recorded by means of a special coordinograph. The accuracy of motions and their coordination decreased. Fine coordination of motions is disrupted at smaller vibration amplitudes than is coarse coordination. Counting and writing tests show an increase in the number of errors and in the time for fulfilling the tasks. The authors note that during short-term vibrations, the latent periods for motions may sometimes even decrease.

The tonus of skeletal muscles changes substantially. V.G. Artamonova and M.F. Stoma (1963) used an Uflands electrotonometer to measure muscle tone in patients with vibration sickness. In 85% of the workers, tonus of the muscles was changed. The authors have established that even physical tension changes muscle tonus less than does vibration. Not very protracted and not excessivly strong vibrations usually increase muscle tonus. General tension of the trunk muscles develops, this being regarded by many researchers as a compensatory protective reaction which diminishes the negative effect of vibration on the organism (Tsuy Chzhun-syan, 1957; Borshchevskiy, Yemel'yanov et al., 1963; Armstrong, 1954, and others). Some authors connect exactly this increase of tonic tension of transversal-striated muscles with the intensification of gas exchange during the first period of vibration (Uglov, 1935*, Lebedeva, 1957; Karchmarzh, 1960, 1962). Sometimes the increase of basic exchange is observed not only during the vibration period itself, but also long afterward (Uglov, 1935, Slonim, 1950, Muller, 1939).*

With prolonged, srong vibration or with generalized forms of vibration sickness, a sharp decrease of the tonus of skeletal muscles was usually observed (Artamonova, Stoma, 1963).

The change of muscular tonus under the action of vibration is also confirmed by electromyographic recordings. I. Ya. Borshchevskiy, M.D. Yemel'yanov et al (1963) recorded the electromyograms of the femoral biceps and quadriceps, biceps and triceps of the shoulder, the sternocleidomastoid muscle, the longus dorsi muscle, and the straight muscle of the abdomen. Vibration with a frequency of 10-70 cps and an amplitude of 0.4 mm caused increased bioelectric /32
activity of the muslces not only of the extremities, but also of the trunk and neck. With a vibration frequency of

* Quoted according to S.I. Karchmarzh, 1960.

10 cps and an amplitude of 0.8 mm, the voltage of biocurrents at first increased, then returned to normal, and after 4 hours of vibration, decreased somewhat. Increasing the vibration amplitude to 1.6 mm (frequency 40 cps) results in rapid depression of the bioelectric activity and a decrease in the amplitude of muscular currents. With repeated vibrations, the changes diminish. M.F. Stoma (1963) and L.V. Donskaya and M.F. Stoma (1960) detected an increase in the amplitude of biocurrents of the sural muscle of a rabbit with an increase of the vibration frequency to 50 cps. They observed, on the electromyogram, groups of pulses that were synchronous with the vibration frequency. Further increase of the vibration frequency causes reduction of myoelectric activity and disruption of synchronization. There is a most effective amplitude of vibration for the level of electric activity of muscles; this amplitude is different for various frequencies. At a frequency of 50 cps, biocurrents of the greatest amplitude originate at any vibration amplitude. This is the limit of lability of the given system. Thus, the bioelectric activity of muscles depends on the vibration parameters. Short, and not very strong vibrations enhance it, while long, intense vibrations depress it. It has been established that the observed reactions are not a result of direct action of vibration on the muscles, but are a reflex reaction of the organism (Donskaya, Stoma, 1960). The mechanism of this reaction is connected with functional changes in the central nervous system at various levels of it. Many researchers have noted here that the above-indicated motor and myotonic deviations are determined by the state not only of the motor analyzer, but also of the vestibular analyzer (Artamonova, Mikulinskiy, 1963; Tsuy Chzhun-syan, 1957; Lebedeva, Vozhzhova, 1963; Andreyeva-Galanina, 1963; Menshov, 1962; Mikulinskiy, 1963; Borshchevskiy, Yemel'yanov et al., 1963).

As already mentioned above, very few special investigations of the action of vibration on the functional state of the vestibular analyzer have been conducted. Often the authors simply mention the appearance of spontaneous labyrinthine symptoms and discuss the changes of excitability of the vestibular analyzer. Sometimes use has been made of qualitative tests such as the digital-nasal test, the test for stability in Romberg's position, for missing the mark, and others /33 (Artamonova, Mikulinskiy, 1963; Usenko, 1961; Ernsthausen, 1950). In some studies the change of vestibular chronaxie under the action of vibration was measured. Thus, V.R. Usenko (1961) established that after 5-minute general vibration (10 cps, 1.5 mm), in persons with high excitability of the vestibular apparatus the chronaxie became shorter, while in persons with weak excitability it became longer. The rheobase in all 4 test subjects diminished. A parallel test for missing the mark showed an increase in the degree of scattering by 48-87%. The author confirms the state of excitation of the vestibular apparatus after vibration. Z.M. Butkovskaya (1959) with a vibration frequency of 30-50 cps, an amplitude of 0.5 mm, and a duration of 5-10 min, detected in humans a reduction of vestibular chronaxie by 20-29% and a decrease of the rheobase by 25-28%. Moreover, on the basis of the thymol test it was established that the effect of vibration lessened the connection between the vestibular and the olfactory analyzers. Bugard and Souvras (1953) point to the increase of vestibular chronaxie under the effect of industrial vibration.

Ye. Ts. Andreyeva-Galanina and A.F. Lebedeva (1955) used the caloric test for investigation of the functional state of the vestibular apparatus in man. After vibration (6 cps, 0.3 mm), in some test subjects the caloric nystagmus became shorter, while in others it became longer.

P.S. Kublanova (1960),during investigation of concrete-mixing workers (daily 3.5 hour vibration at 40-50 cps. 0.4-0.9 mm) used calorization and slow rotation as test irritants. She detected decreased excitability of the vestibular analyzer with the change of duration, and partial or total prolapse of the rapid component of nystagmus -- a symptom of "floating" of the eyes.

By means of a rotation test (Markaryan's electrically rotating chair), S.S. Markaryan (1959) and I.A. Borshchevskiy, M.D. Yemel'yanov et al., (1963) investigated the functional state of the vestibular analyzer under the action of vibration of various parameters (10, 40, and 70 cps; 0.4, 0.8, 1.6, and 2.4 mm). Taken into consideration was the general state of tested subjects, the duration of the illusions of counter-rotation, post-rotational nystagmus, and vegetative reactions (pulse, respiration, arterial pressure, etc.). Rotation (10 revolutions per 20 sec) was conducted in the planes of the horizontal, the frontal and the sagittal semicircular canals. It was found that vibration of various parameters in some degree inhibits vestibular reactions. During vibration and afterwards, these reactions, in response to adequate stimulation of vestibular apparatus by rotation, were somewhat less expressed than before vibration. Increase of vestibular reactions to rotation after vibration was observed only in individual cases.

We could not find, in the accessible literature, any works with the application of experimental dosed stimulation of the otolithic part of the vestibular analyzer under the action of vibration. In the opinion of many researchers, the vestibular disorders observed under vibration result not so much from changes in the peripheral labyrinth, as from changes in the central paths and structures of the vestibular analyzer and its connections with other analyzer systems. The degree of manifestation of vestibular reflexes depends /34 more on the state of the cenrtal regulatory mechanisms, on the central section of the analyzer (Usenko, 1961; Voyachek, 1946; Shpil'berg, 1960; Butovskaya, 1957, 1959; Andreyeva-Galanina, Butovskaya, 1960; Temkin, Kublanova, 1960). P.S. Kublanova (1960) is of the opinion that shifts observed after rotation such as vertigo, loss of equilibrium, hypo-reflexion, instability of excitation, dissociation between caloric and rotational excitability, disharmonic misses of mark in an indicator test, symptoms of floating of the eyes, indicate central vestibular disruptions.

P.I. Shpilberg (1962) speaks of the presence, in vibrational sickness, of a pathological process in the region of the central vestibular nuclei (in the layer of Varoliev's bridge). This process develops under the effect of prolonged and strong irritations of the vestibular apparatus. Gradual changes occur in the functional state of the reticular system of the brainstem and in the related diencephalic region. Cortical-subcortical correlations are disrupted.

A.M. Volokov et al.(1960) detected exaltation of the d-rhythm in the temporal region of the cortex, which is subsequently replaced by depression of this rhythm in the temporal-occiputal and temporal-frontal regions (vibration with a frequency of 50 cps and an amplitude of 0.3 mm was applied). Sometimes the phenomenon of super-excitation with gradual development of a deep inhibitory state was observed, subcortical formations being involved in these processes. The chronaxie of the vestibular nerve became longer immediately after vibration; there was a tendency toward distortion of the force relations.

G.I. Rumyantsev (1960) detected considerable shifts of bioelectric activity in the temporal and motor regions of the cortex in concrete mixer operators under the action of vibrations with a frequency of 40-100 cps and an amplitude of 0.05-1.3 mm. A decrease of the alpha-rhythm potentials, with depression phenomena, was observed. In some of the test subjects diffuse excitation in all regions of cortex was observed, while in others the excitation process had a stagnant character, with a tendency toward concentration in the locomotor and acoustic regions. Stagnant foci of excitation appeared in these regions. The excitability of vestibular nerve increased. Adey et al (1961) observed the propagation of spasmodic discharges in deeply seated structures of the temporal region and the brainstem during and after vibration (10-30 cps, 0.5-5 mm).

Central vestibular disruptions result from general affection of the nervous system, which is very typical for vibrational action (Temkin, 1960).

At present it can be regarded as proven that vibration /35 (sufficiently long and strong) affects mostly the central nervous system with a complex of neurodynamic and microfocal disturbances. Affected are various sections of the cerebrum and, selectively, of the stem-diencephalic region. The basis for multiform shifts during vibration is functional weakening of the cerebral cortex and the appearance of stable foci of excitation on the periphery and in the centers (Andreyeva-Galanina, 1960; Luk'yanova, 1964a; Kuznetsova, 1964b; Mel'kumova, 1960; Artamonova, Zuyev, Khaymovich, 1963). This problem is dealt with in extensive literature, a detailed analysis of which is outside the scope of the present review. On the basis of that literature, the character of functional changes in the central nervous system under the action of vibration can be schematically represented as follows.

Vibration strengthens the flow of pulses from various receptors, for which it is an adequate or an inadequate irritant. Correlation between the basic nervous processes is disrupted. During the first period an excitatory process prevails, which later begins to diminish. Inhibition gradually develops in the cerebral cortex, later acquiring a diffuse protective character. Inertia of the basic nervous processes, the disruption of force relations, and phase phenomena are very characteristic of such states (Andrianov, 1960; Borshchevskiy, Yemel'yanov, Koreshkov, 1958; Butkovskaya, Koryukayev, 1963; Gurovskiy, 1959; Terent'yev, V.L., 1959; Luk'yanova, 1964a; Lebedeva, 1953; Abramovich-Polyakov, 1962; Karpova, 1963, and many others).

Against the background of general inhibition in these or those cortical regions (for example, motor, acoustic), stagnant foci of excitation appear (Vozhhova, Lebedeva, 1960; Rumyantsev, 1960; Volkov, Kondaurova, Rumyantsev, 1960; Shpil'berg, Mel'kumova, 1960, etc.). Conditioned and unconditioned reflexes change, are distorted, or disappear

(Butkovskaya, 1957; Zuyev, 1960; Skachedub, 1957; Mikheyeva, 1955; Shabalin, 1962; Livshits and Meyzerov, 1960a; Gatterson et al, 1962, and others). Typical changes appear on the electroencephalogram: depression of the alpha-rhythm, appearance of slow waves, etc. (Borshchevskiy, Yemel'yanov, et al, 1963 , Ginzburg, Cheremnykh, 1961; Volokov, Kandaurova, Rumyantsev et al, 1960; Volkov, 1959; Rumyantsev, 1960; Drogichina, Metlina, 1962; Shpil'berg, Mel'kumova, 1960, and others). The coordinating influence of the cortex on the subcortex weakens. Multiform sympathetic reactions are manifested. Some changes are connected with the formation of stagnant foci of excitation in these or those segments of the spinal cord (Pavlova, 1958; Malinskaya, 1962; Andrianov, 1958; Andreyeva-Galanina, 1960; 1963; Kuznetsova, 1964b). The muscle tonus is redistributed and muscle tension develops due to the additional load during vibration (Borshchevskiy, /36 Yemel'yanov et al, 1963). The functions of many other organs change. On the periphery, the sensitivity of a number of receptors gradually decreases, mainly of those which are connected with the perception of vibration ((Borshchevskiy, Yemel'yanov et al, 1963). Thus, under the effect of vibration, substantial shifts of a reflex character occur in almost all functional structures.

In conclusion, it may be noted that great varialibity and dispersion of indices, and lability of changes, are typical for vibrational action (Vozhzhova, Lebedeva, 1960; Temkin, 1960; Usenko, 1961, Lebedeva, 1963; Andreyeva-Galanina, Lebedeva, 1955 and others).

At the same time, the effects of vibration often are characterized by particular stability; a return to normal is sometimes not observed for a long time (Vozhzhova, Lebedeva, 1960; Lebedeva, 1963; Lebedeva, Vozhzhova, 1963; Temkin, 1960; Shcherbak, 1907; Skachedub, 1957; Tsuy, Chzhun-syan, 1957, 1960; Borshchevskiy, Yemel'yanov et al, 1963; Andre eva-Galanina, Butkovskaya, 1960).

In most cases, adaptation of the organism to vibrational irritation takes place (Skachedub, 1957; Andreyeva-Galanina, Lebedeva, 1955; Artamonova, Zuyev, Khaymovich, 1963; Gurovskiy, 1959; Labadze, Khvatasi, 1963, and others). Sometimes there develops fatigue of the nervous formations which perceive the vibration (Borshchevskiy, Yemel'yanov et al, 1963). However, the problem of adaptation to vibration is a complicated one; the appearance of adaptation is individual, and depends on many conditions. In some cases, adaptation develops very slowly or not at all (Andreyeva-Galanina, Lebedeva, 1955; Butkovskaya, 1959: Borshchevskiy, Yemel'yanov, Koreskhov, 1958; Luk'yanova, 1964b, and others). There have been cases of sensitization to vibration, and of the summation of vibrational irritations (Shpil'berg, 1962;

Vozhzhova, Lebedeva, 1960; Borshchevskiy, Yemel'yanov, et al 1963).

The Effect of Penetrating Radiation on the Functions of the Vestibular Analyzer

The problem of the effect of radiation on vestibular functions is to a considerable degree part of the general problem of radiation injury to the central nervous system (Lebedinskiy, Grigor'yev, 1961; Petelina, 1958; Moskovskaya, 1958; 1959; Sveshnikov, 1963; Sevan'kayev, 1964, and others). Much literature is dedicated to this problem and the results are generalized in numerous reviews, monographs and articles (Lebedinskiy, Nakhil'nitskaya, 1960; Livshits, 1956; 1958; 1961a; Livanov, 1962; Tsypin, 1963; Grigor'yev, 1963; Biryukov, 1957; Gorinszontov, 1955; Gus'kova, 1960; Livanov, 1956; Tsypin, Grigor'yev, 1960; Ellinger, 1941; Lea, 1946, /37
and many others). There are relatively few special investigations of the effect of penetratiing radiation on the vestibular analyzer; almost all of them are also included in the recent reviews of this problem (Sevan'kayev, Sveshnikov, 1963; Sevan'kayev, 1964).

The above-indiciated circumstances allow information available in this field to be presented here very briefly and schematically.

The first information on vestibular disturbances caused by radiation was obtained from clinicians who observed changes of the excitability of the equilibrium organ and the symptom complexes of labyrinths after radiation therapy of the head or nearby regions (Voyachek, 1960*, Donato, 1926*; Moskovskaya, 1959). Subsequently such deviations were often encountered in the chronic form of radiation sickness in persons working in contact with x-rays and other types of ionizing radiation. The normal correlation of sensory, somatic, and vegetative reactions was changed. Multiple spontaneous symptoms of vestibular disturbances appeared: nystagmoid twitching, decrease of muscular tonus, disruption of static and locomotor correlation, general motor inhibition, attacks of vertigo with disruption of statics and various photopsias, opticovestibular disorders. Sometimes the dissociation of caloric and rotational nystagmus was observed. The phenomena increased with change of body position (Kurshakov, 1954**; Blagovshchenskaya, 1956; Titov, 1957; Golodets, 1954, et al.). Experimental research

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* Quoted according to N.V. Moskovskaya, 1959.
** Quoted according to A.V. Sevankayev, 1964.

on animals discloses functional and morphologic changes in the structures of the vestibular analyzer after local and general irradiation. Morphologic changes frequently taking place were hyperemia, hemorrhages, and inflamation of the middle and inner ear. Small-celled inflamatory infiltration, dilation of blood vessels, and defects of nerve fibers and ganglionic cells were observed (Thielemann, 1929; Marx, 1909*; Levy, Quastler, 1962). N.I. Ivanov (1957) notes that local and general irradiation of rabbits and guinea pigs in relatively large doses result in major atropic and degenerative changes of sensitive formations of the inner ear. Degenerative and inflammatory changes occur not only in the peripheral receptor, but also in vestibular nuclei of Schval'be, Deiters and Bekhterev (Zlotnikov, 1959; 1961). P.N. Mil'shteyn (1939), after having inserted for 2-10 days a capillary with radium emanation (10-30 microcuries) into an oval window in rabbits, observed the appearance ot exudate under the basilar membrane /38
of the utriculus in the place where the branch of the vestibular nerve passes. A.I. Loptako (1939) detected in mice, after irradiation with large doses, major degenerative and atrophic changes in the labyrinth, all the way to cutoff of the sacculus otoliths. The author notes that the cochlea and the sacculus are injured more often than are the semicircular canals and the utriculus.

Spontaneous symptoms of functional affection of the labyrinth in experimental irradiation of animals were absent only in rare cases (Brown, Cibis, Pickering, 1955). Most researchers point out the occurrence of vestibular disorders in the case of general or local irradiation (of the head and its individual parts) in animals pigeons, hens, white mice, rats, rabbits, cats, hamsters, dogs, monkeys. The authors usually observed spontaneous nystagmus, progressive apathy and ataxia, periodically changing to clinical rotatory motions, inclination and turning of the head, tremor, disruption of equilibrium and orientation in space (Khilov, 1927; Minayev, 1962; Obersteiner, 1904; Thielemann, 1929; Ewald, 1905; Ross et al, 1954; Clemente et al. 1958; Gerstner, Kent, 1957; Berg, Lindgren, 1958; Brightman, 1959; Ming-Tsung, Peng et al.,1958; Quastler, 1957, Tognacca et al.,1963).

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* Quoted according to A.V. Sevankayev, 1964.

Gerstener and Kent (1957) connect the observed phenomena with local vestibular-cerebellar disturbances, and indicate the possible participation also of the peripheral apparatus of the inner ear. Quastler (1957) and later Levi and Quastler (1962), singled out from general motor disorders the syndrome of spatial disorientation. By experiments with strictly local irradiation (a directed 3-mm beam of rays), or protection of the region of the inner ear with subsequent histological control, the authors prove the labyrinthine etiology of this syndrome. They consider that, with their methodology of experimentation, the vestibular nuclei, the brainstem, and the cerebellum were excluded from the region of irradiation effect. With large doses, radiation motor-coordination disorders sometimes remained for a long time, or even became irreversible (Minayev, 1962; Quastler, Levi and Quastler, 1962; Tognacca et al. 1963). Special tests for study of the radiation effect on the functions of the vestibular analyzer were rarely undertaken. Rotary and caloric tests were used clinically by N.V. Moskovskaya (1958, 1959). She also applied the indicator test and the test for stability in Romberg's position. The author has detected an increased excitability of the vestibular analyzer during and after irradiation in patients who were receiving X-ray treatment for tumors (5000-12000 r in the region the neck or thorax). V. V. Petelina (1957) observed in cats, after irradiation with a dose of 400 r, a decrease of the time of prostrotational /39
nystagmus. The changes were of a wave type; complete normalization was not attained even after 30 days.

Wave-type changes were also incurred by conditioned reflexes from the vestibular analyzer (in dogs in response to rotation), but they were restored more quickly. The degree of manifestation of the disturbances was the same as for reflexes from other analyzers.

A large series of studies with the application of dosed stimulation of the vestibular apparatus by rotation (angular acceleration) was conducted by Yu. G. Grigor'yev and co-workers (Grigor'yev, 1963; Sveshnikov, Sevan'kayev, 1962, Sevan'kayev, 1963a and b; Grigor'yev, Sveshnikov, Sevan'kayev, 1964; Sveshnikov, 1963; Sevan'kayev, 1964). An evaluation was made of the threshold sensitivity and reactivity of the vestibular analyzer with objective recording of vestibulosomatic (nystagmus) and vestibulo-vegetative reflexes (respiration, pulse, blood pressure). Sometimes the caloric test was used in parallel. Investigations were made of the change of vestibular functions in rabbits and dogs under the action of various doses of protons, X-rays and gamma rays. It was established that the sensitivity and reactivity of the vestibular analyzer often increase with small doses of radiation (50-100 r), while with large doses (200-10,000 r) they usually decrease. The reduction of reactivity was accompanied in many cases by disturbance of the normal force relations and phase states. The development of phase phenomena and the propensity of the organism to paradoxical vestibular reactions under the action of irradiation was also noted by a number of other authors (Petelina, 1957, 1959; Nesterenko, 1964; Golodets, 1964; Zlotonikov, 1958). Application of pharmacological substances (caffeine, bromine, aminasine, phenathin, chloral hydrate) exerts a corrective action on the change of vestibular reflexes (Petelina, 1958; Moskovskaya, 1958, 1959). The above-indicated circumstances testify to the fact that the central sections of the vestibular analyzer and of the central nervous system as a whole participate in labyrinthine radiation effects (Petelina, 1957, 1958; Zlotnikov, 1959; Lebedinskiy, Grigoryev, 1961; Moskovskaya, 1958, 1959; Golodets, 1964; Sveshnikov, 1963; Sevan'kayev, 1964, and others). Concerning the role of higher sections of the central nervous system in the performance of vestibular functions, the major importance of cortical regulation and interaction of the centers and the peripheral apparatus of the equilibrium organ, there is a large body of literature, the analysis of which is outside the scope of the present article (Ageyeva-Maykova, 1953; Aspisov, 1946; Balkovskaya, 1959; Blagoveshchenskaya, 1962; Budo, 1959; Zhirmunskaya, Ioselevich, 1951; Zhukovich, 1954; 1956; Zlotnikov, 1958; Kalinovskaya, Mayorchik, 1952; Krestovnikov, Yarotskiy, 1938; Kulikov, 1960; Medvedovskiy, Nevskiy, 1940; Pinchuk, 1948; Tyumyantsev, 1926; Khechinashvili, 1951; Khilov, /40 1951, 1952; Yaroslavskiy, 1950; Yarotskiy, 1954; Magnus, 1924, Silverstein, 1962; Spiegel 1934 and others).

Study of the effect of radiation on the vestibular functions has been conducted on various animals with varying doses and conditions of irradiation. The dependence of vestibular radiation effects upon the radiation dosage is mentioned by many authors; there are also several special studies dealing with this problem (Sevan'kayev, 1963, 1964; Levy, Quastler, 1962, and others). Regarding the conditions of irradiations, there are indications only of the effect of general and local radiation. Other conditions of irradiation, particularly the dose strength, are often not even mentioned. Concerning the effect of the time factor on reactions of the vestibular analyzer to radiation, we could not find a single special study in the accessible literature. There are only several remarks on fractionized effect.

I.A. Lopatko (1939), studying morphological changes in the inner ear after general and local, single-stage and fractional irradiations of white mice, points out that local (single-stage and fractional) irradiations in the region of the ear cuase greater changes than general irradiations in large doses.

Levi and Quastler (1962) irradiated the inner ear of hamsters in single stages and in several fractions. They established that, depending on the value of the fractions and the intervals between them, there is observed a varying degree of weakening of the effectiveness in fractionizing the exposure. The total dose somewhat exceeded the threshold dose in a single-stage exposure. The authors also note that the effect of fractional irradiation may not necessarily be of the same etiology as in single-stage irradiation. A.A. Sveshnikov (1963) subjected dogs to general gamma irradiation in a dose of 200 r with single-stage and fractional (every second day, 9 r per day)exposure. In fractionalized irradiation, changes of the labyrinthine functions were less expressed than in single-stage action. We were unable to find any other information concerning the role of the time factor in radiation reactions of the vestibular analyzer.

It is noteworthy that all vestibular tests, applied by various authors, were addressed mainly to the semicircular canals and characterized the functional state of the cupular part of labyrinth. Changes of otolothic reactions under the action of penetrating radiation have not been a subject of special studies; the corresponding tests were not used.

The Complex Effect of Radiation and Dynamic Space-Flight Factors /41

Most often, including during the conditions of space flight, the organism encounters the action not of a single irritant, but of an entire complex of various factors. The interaction of these factors may substantially change the effect of each of them and may cause unusual responses. In this connection, the problem of complexity in the effect of space-flight factors is named as one of the basic directions in scientific research on the mastering of space (Yazdovskiy, 1964). In flights of long duration, in passing through the natural and artificial radiation belts of the Earth, and in the case of solar flares, the astronauts may be exposed to real radiation hazard. The problem of the complex action of radiation and of non-radiational factors acquires not only theoretical, but also practical importance. This problem has been the subject of numerous scientific studies. However, the interaction between irradiation and mechanical injuries, burns, and blood losses has been studied most. In a number of research efforts, radiation was combined with the shock state, with the action of blast waves, the influence of high and low temperatures, or with a physical or functional load. The above-indicated complex actions usually led to a reciprocal increase of the harmful effect of the individual components. In some cases there was either a decrease of the harmful effect, or faster normalization of the disrupted functions. The basic material, accumulated in the scientific literature concerning the combined action of radiation and the above-mentioned non-radiational factors, has been generalized in the respective reviews and does not require additional analysis (Khromov, 1959; Sokolova, 1962; Livshits, 1964, and others). The problem concerning the joint action of radiation and such important dynamic space-flight factors as acceleration and vibration has been insufficiently studied. The literature contains information concerning only a few such special investigations. In experiments with white rats and mice it was established that the accelerations (up to 20-25 G) while centrifugating the animals before, during, and after irradiation in doses of 600-1000 r, increase resistance to radiation rather than aggravating the course of radiation sickness. Here the protective effect of accelerations is comparatively small and decreases with increase of the radiation dose, and at a dose of more than 750 r it sometimes entirely disappears (Lazar', 1963; Ivanov, Zhikov, Molchanova, 1962; Davydov, Antipov, Konnova, Saksonov, 1965; Zellmer, et al., 1963; David, 1962). Some of these research works also note less weight loss and less changes in the peripheral blood after complex action than after isolated action of the individual factors. Other authors, also experimenting on rats and under similar /42 parameters of irradiation and centrifugation, did not detect any difference in the survival of animals in the case of isolated or combined effect of the factors (Lyle, 1961; Taylor, 1960). A number of Soviet and foreign geneticists have investigated the changes in chromosomal apparatus of plant and animal cells under the complex effect of accelerations and penetrating radiation on the organism. Centrifugation of microspores of the spiderwort (Tradescadentia) during radiation intensifies the effect of radiation and increases the number of chromosomal rearrangements. Action of G-forces before radiation weakens the radiation effect. Postradiational centrifugation either does not affect, or increases the effectiveness of radiation action (Sax, 1943; Wolf, Borstell, 1954). G.P. Parfenov detected an intensification of the mutagenic effect of radiation (500 r) on the number of dominant lethals in the vinegar fly (Drosophila) with the preliminary action of accelerations (40 or 4000 G). In centrifugation after radiation, the effects of the two actions were summated.

The protective effect of acceleration (8G), applied one hour before irradiation (100 r), has been observed in a series of investigations by M.A. Arsen'yev and co-authors (1956a). The frequency of radiation-caused chromosomal rearrangements in the bone marrow and spleen cells of mice decreased within an interval of 30 minutes to 2 days after action.

A considerable modifying effect of preceding centrifugation on radiation shifts of conditioned-reflex activity in rats has been shown by N.N. Livshits and Ye. S. Mayzerov (see article in the present collection).

Concerning the influence of vibration on radiation effects, only the work of A.N. Ganshina (1961) has been known up to now. Four-hour vertical vibration (70 cps, 1 mm) of rats considerably intensifies the pathomorphological effect of acute irradiation (400 r) and does not substantially change the effect of fractionized irradiation (4 times at 100 r, every second day). Recently a series of experiments was performed in N.N. Livshits' laboratory, dealing with the complex action of general vibration (70 cps, 0.4 mm) and radiation in sublethal and minimally lethal doses on some functions of the central nervous system. It was demonstrated that vibration changes considerably the effect of acute irradiation on conditioned reflex activity (Livshits, Meyzerov, 1966b), on the oxidation processes in cerebral tissues (Luk'yanova, 1964 b), and on the value of the latent period of the unconditioned passive-defensive flexoral reflex (Kuznetsova, 1964b). Yu. A. Demin (1963) has found that with the complex action of vibration (70 cps, 0.4 mm) and irradiation (50 and 100 r), the total amount of disturbed mitoses in the nuclei of bone-marrow cells of mice did not change substantially, as compared with such an amount with irradiation alone. However, the spectrum of disturbed mitoses demonstrates a substantial difference: /43
in complex action there is a smaller number of cells with chromosomal bridges, while the number of cells with chromosome adhesions, characteristic of vibration, increases.

Other researchers also note either the protective (Arsen'yeva et al. 1965 a & b) or the enhancing action (Zhukov-Berezhnikov et al. 1965) of vibration on the genetic effects of radiation.

We could not find, in the accessible literature, any investigations on the complex action of irradiation and vibration or centrifugation on the vestibular analyzer. There is only the work of V.S. Nesterenko (1964), in which it is shown that with gamma-irradiation of rabbits in doses of 800 r, the sensitivity of the vestibular apparatus to Coriolis accelerations decreases. However, what is considered here is not so much the mutual effect of two strong factors, but rather the radiation-caused change of the reactions of the vestibular apparatus to adequate stimulation. A.F. Lazar' (1963) mentions in a brief remark the decrease of motor-coordination disturbances in rats caused by centrifugation (10 or 25 G; 10 min) with preliminary or subsequent irradiation by a 750 r dose.

In our works (Apanasenko, 1964, 1966a) we have shown that vibration substantially changes the effect of irradiation on the electromyographic characteristics of the vestibulotonic reflex. These interrelations between the effects of the acting factors were complicated and multiform. They could be evaluated neither as simple protection, nor as the reciprocal intensification of injurious action. The effect of the complex action usually showed in the earlier period, that of irradiation. Also observed were cases of the cancellation of oppositely directed effects, intensification of the effect of one factor by the oppositely directed effect of another, the predominance, in one group of experimental animals, of vibrational effects and in another group - of radiation effects, etc. It was also shown that the effects of prolonged irradiation change under the influence of vibration in a somewhat lesser degree than do the corresponding effect of acute irradiation. Radiation effects are also substantially modified by preliminary centrifugation (see article in this collection). Most frequently of all, the effects of acceleration dominated and masked the radiation reactions almost up to the moment of death of the animals. Some other types of the interaction of component factors were also noted; however, on the whole the relations are here less mutliform than in the combined action of irradiation and vibration. No other information on the complex influence of radiation and non-radiation factors on the vestibular functions is available to us.

Analysis of the available bibliographic material shows the following:

1. The vestibular analyzer (and particularly the otoliths) is responsible for the appearance of a number of disturbances of motor coordination and spatial orientation under the conditions of parabolic and orbital flights. The same system also plays the leading role in the development of the motion sickness syndrome.

2. Neither the isolated, nor the combined action of space-flight factors on the vestibular analyzer has yet been sufficiently studied. Nevertheless, many of these factors are adequate for the nonacoustic labyrinth and are selectively perceived by it.

3. Special investigations of the functional state of the otolithic part of the vestibular analyzer under the action of space-flight factors are almost entirely nonexistent.

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